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Consequences of shortened hunting seasons by the Birds Directive on late winter teal *Anas crecca* abundance in France

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The European Birds Directive (EBD) prevents hunting during spring migration, primarily to facilitate birds' use of habitats before and during the prenuptial journey. In line with the EBD requirements, the hunting season for waterfowl in southern France was shortened by two months during February–March since the mid-1950s. However, consequences of such hunting bans for late winter habitat use have not been evaluated. We investigated a 55-years dataset from a major international wintering ground to assess whether the EBD-related changes in hunting legislation have led to increased regional teal *Anas crecca* numbers during late winter. Teal abundance in the Camargue during late winter increased over the last decades: the ban on hunting in February was the best predictor of teal numbers during that month, leading to a sudden 50% increase in relative abundance. In March a more gradual temporal increase since the mid-1960 was instead recorded. Whether the increase in teal during late winter resulted from locally wintering birds or those from elsewhere stopping in the Camargue cannot be discerned. Nonetheless, the increase in teal numbers supports the basis for the EBD, in that a ban on hunting during late winter is associated with a greater use of habitats during this crucial part of the annual cycle, especially in February.

Keywords: disturbance, hunting regulation, phenology, spring migration, waterbirds

A major regulation from the European Birds Directive (EBD) is that migratory birds should neither be hunted during breeding seasons nor spring migration (Article 7; European Commission 2008). To allow member states to adjust their hunting season dates to the annual life cycle of gamebird species, the European Commission regularly updates the Key Concept Document, which provides the beginning and end dates of the spring migration and breeding seasons for each species by each country (<https://ec.europa.eu/environment/nature/conservation/wildbirds/hunting/key_concepts_en.htm>). The ban on hunting when spring migration starts aims to protect birds from the likelihood of hunting mortality being additive to natural mortality and enhance reproductive value of individuals (Kokko 2001, Williams et al. 2002, European Commission 2008). Another reason is to allow birds to use winter quarters and migration stopovers to their full potential to build body reserves for the impending migration and breeding season (European Commission 2008). Indeed, migratory birds require lipid and proteins during that part of the year (McLandress and Raveling 1981, Lindström and Piersma 1993).

Hunting seasons for waterfowl have been shortened since the 1970s, especially in France, with implementation of the Birds Directive and improved understanding of the birds' annual cycles. The gradual shortening of the hunting season mostly has occurred through earlier ending dates rather than later openings. In southern France, March hunting was gradually banned in the mid-1970s, and February hunting around year 2002 (Fig. 1). Earlier analyses have confirmed that common teal *Anas crecca* (hereafter teal) initiate spring migration from France during the first 10 days of February (Guillemain et al. 2006).

Evidence exists that disturbance caused by human activities, especially hunting, can affect migratory birds (Madsen and Fox 1995, Perry and Deller 1996, Tamisier et al. 2003). In waterfowl, Väänänen (2001) demonstrated that the open-

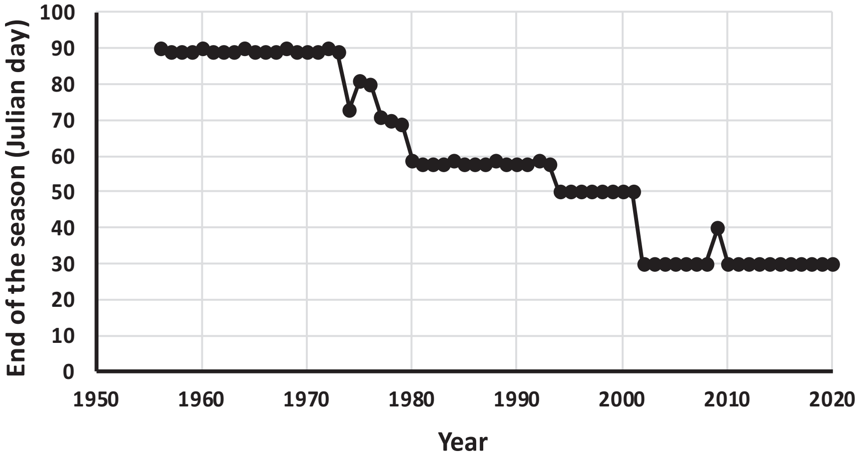

Figure 1. Changes in the annual closure date of the teal hunting season in Camargue, southern France (based on Guillemain and Elmberg 2014 plus additional annual data courtesy of Jean-Yves Mondain-Monval, OFB). Days indicated as Julian date from the 1 January each year.

ing of the season in Finland during August initiated duck fall migration and dispersed remaining individuals toward refuge areas. The creation of a large network of nature reserves in Denmark also has increased local numbers of birds at those sites, large enough to be visible in total numbers of individuals at the national scale during autumn migration (Madsen 1998). In the Camargue, southern France, Tamisier and Dehorter (1999) and Brochet et al. (2009) hypothesized that hunting disturbance restricted access to nocturnal foraging grounds and was therefore limiting waterfowl numbers during the wintering period.

However, environmental and intrinsic (e.g. hormonal) cues for duck migration differ among seasons. In autumn, ducks move south with declining photoperiod and dynamics of weather and food resources, with some individuals migrating ahead of cold temperatures and snow cover, while others may linger until conditions become severe (Schummer et al. 2010, Dalby 2013, Notaro et al. 2016). Additionally, increasing abundances of ducks are wintering farther north in Europe and North America (Guillemain et al. 2013, Schummer et al. 2017, Meehan et al. 2021). However, in spring, ducks migrate toward breeding grounds as soon as physical and physiological conditions are suitable (i.e. ice-free, sufficient nutrient reserves; Batt et al. 1992, Elmberg et al. 2005). Further, food resources for waterfowl in the northern hemisphere get depleted during spring migration relative to other seasons; plants have not yet emerged or germinated, and invertebrates often remain relatively inactive (Arzel et al. 2009, Straub et al. 2012). Therefore, determining effects of late winter hunting closure on habitat use by ducks is important because this period is considered a nutritional and temporal bottle-neck for these birds but has not been evaluated.

Currently, the EBD stands mostly on theoretical grounds, with limited field tests of its efficiency in allowing a better late winter habitat use by migratory birds. The aim of our paper is to test whether changes in hunting legislation with earlier season closure correlated with increased regional bird numbers during late winter. Since the beginning of the International Waterbird Census in the mid-1960s, the Camargue has been the most important wintering region for waterfowl in France, with total numbers over 100 000 individuals in January 2020 (Hémery et al. 1979, Schmaltz et al. 2020). We used waterfowl counts to test our aforementioned correlational hypothesis. Our is not a simple case study, but has the potential to illustrate patterns of change for wintering grounds/spring stopovers in general, because the change in legal hunting dates in Camargue followed national rules and a general trend in Europe. We focused on teal because it is the most abundant purely wild duck in the region (some mallard *Anas platyrhynchos* are released hand-reared birds; Champagnon et al. 2013, Guillemain et al. 2016). We assessed whether their abundance during February and March changed over the years in a gradual fashion over the entire study period, showed a step change after hunting was banned, or changed at a different rate after installations of full hunting bans in 1980 and in 2002.

Methods

We used aerial counts of waterbirds in the Camargue, a consistent ecological entity formed by the Rhone river delta in southern France (ca 43°30′N, 04°35′E). Censuses were conducted monthly from September to March 1964–2019 (n = 55 years), with only 42 missing monthly values (ranging from nine missing years in March to only two in January; Appendix 1). Only three observers recorded bird numbers over the 55 years, each of them training the successor: Alain Tamisier, 1964–2001; Michel Gauthier-Clerc, 2003–2012; Jean-Baptiste Mouronval, 2013–2020, allowing reliability of surveys through time (Vallecillo et al. 2021). Each month a ca 4–6 hours flight was performed to cover all known day-roosts of ducks in the delta. As new day-roosts appeared over the years, the flight path was gradually adjusted. Bird numbers were counted by forcing them to take flight when necessary (sometimes by circling over a given wetland; Fig. 2), recorded on a voice recorder distinguishing the number of individuals per species per wetland. As opposed to North America where dabbling ducks often use agricultural land during the day (Pearse et al. 2012, Davis et al. 2014), European dabbling ducks almost exclusively remain on large open

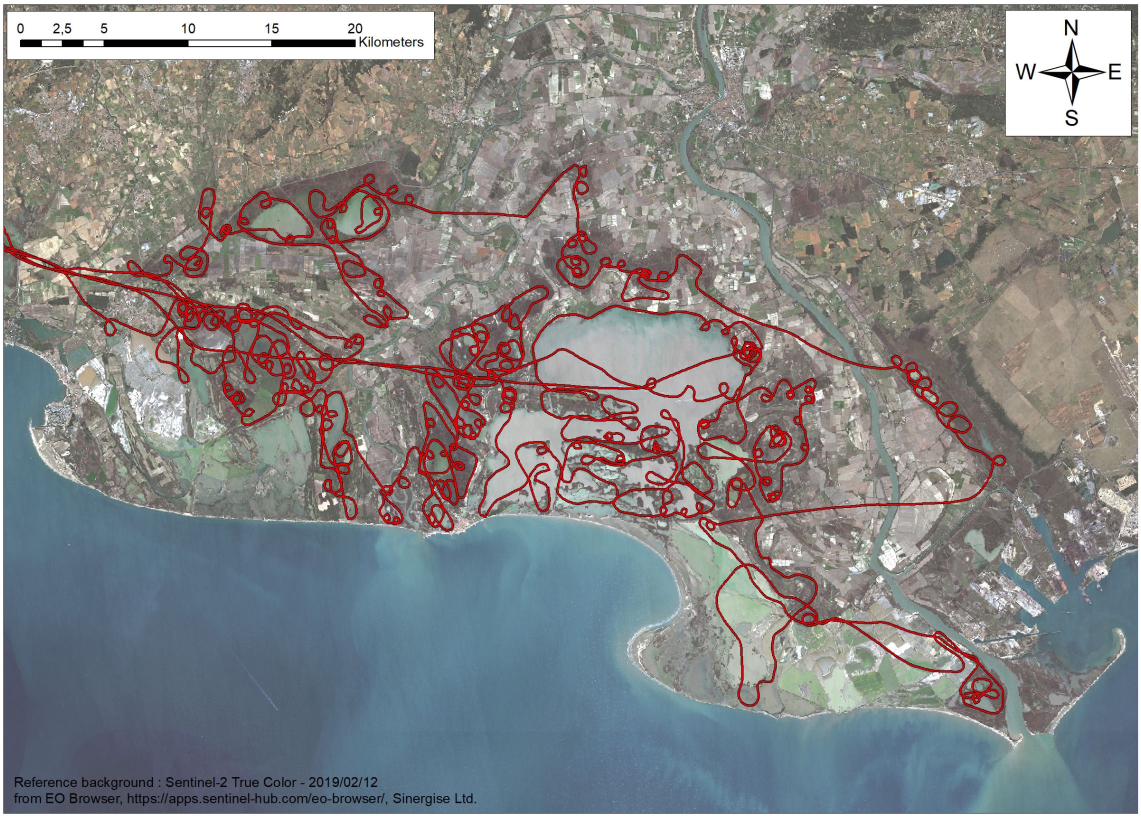

Figure 2. Aerial waterfowl survey path over the Camargue delta (here 14 February 2019). The survey covers all known waterfowl day-roosts, sometimes circling over a given wetland to properly count the number of individuals.

waterbodies during daylight hours, especially in the Camargue where teal gather year after year at traditional wetland sites and not on farmland or salt production areas (Tamisier and Dehorter 1999). The data used in this study were the total number of wintering ducks over the whole 100 000 ha of the delta. As such, the data were a population index that we assumed was not confounded by redistribution of local individuals from diverse local habitats with different detection probabilities or survey coverage (Pearse et al. 2008). The mid-January counts constituted the information provided to Wetlands International for the international waterbird census (Schmaltz et al. 2020).

Our analysis focused on teal because it is the most heavily hunted duck species at the national scale and in the Camargue, where they represent 40–45% of the annual duck bag (Aubry et al. 2016, Tamisier and Dehorter 1999; mallard were excluded). Teal is a strictly migratory bird and also the most consistently abundant purely wild species in the Camargue duck community; they account for 49.46% ($\pm$ 8.67 SD, $n=51$ years) of the total number of dabbling ducks counted during mid-winter (mallard excluded), with a mean of 26 640 teal $\pm$ 11 898 SD in January over the last 54 years and a record 81 500 teal in November 2005.

Wintering waterfowl numbers may show great fluctuation from year to year owing to changes in environmental conditions, especially weather at global flyway scale (Ridgill and Fox 1990) and local food abundance (Hamdi et al. 2012). Changes in observers during the aerial survey, even if they did not occur often in Camargue, may have translated into significant observer effects causing changes in recorded bird numbers (Dervieux et al. 1980, Vallecillo et al. 2021). We therefore calculated the proportional number of teal during each of these months compared to the number recorded in December of the same season (hence by the same observer), which traditionally represents the peak abundance for this species in the area (Fig. 3). Proportions were logit-transformed (Warton and Hui 2011) and tested with Kolmogorov–Smirnov tests for normality ($d=0.146$ and $d=0.073$ for February and March data, respectively, $p > 0.20$). On one occasion (winter 2008–2009) the number of teal in February was greater than the number in December (proportion $=1.09$), preventing logit transformation. This value was bounded to 0.99 (hence logit value $=4.595$). Because this occurred in a year when February hunting was banned, if anything such bounding would have reduced our ability to detect an effect.

We then constructed, separately for February and March data, an initial model to explain changes in the relative abundance of teal depending on relative abundance the previous year (to account for autocorrelation), year (to test for long-term trend), hunting (a binary variable before/after the ban in 1980 and 2002 for March and February, respectively, to test for a change in mean abundance) and year $\times$ hunting (to assess whether the slope of any trend changed after hunting got banned). From this full parameterization a stepwise backwards model selection procedure was used to

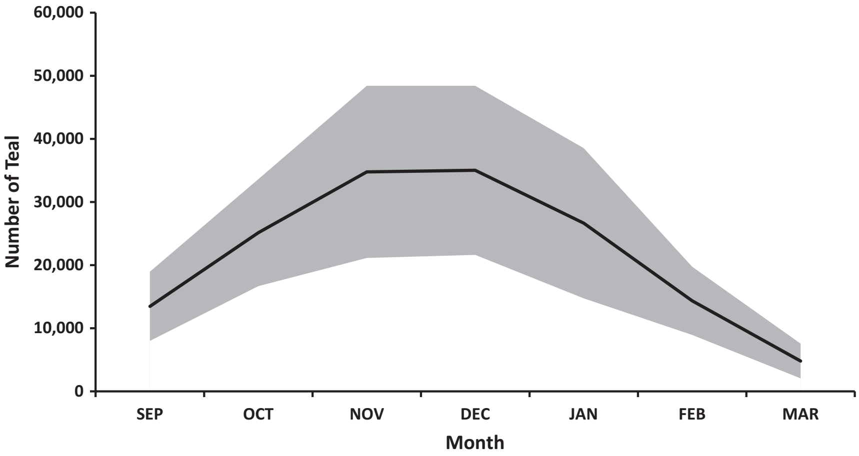

Figure 3. Mean number of teal present per month in Camargue during winter. The grey area shows the mean ± 1 SD; n = 47 (March counts) to 54 (January counts) years.

gradually remove non-significant terms. The statistical analyses were conducted with Statistica 10.0 (Statsoft 2011).

Results

The best model to explain changes in annual abundance of teal in March relative to numbers in December only retained an effect of year, showing a significant linear increase over the years ($\text{Logit}_{(\text{Teal abundance})} = -43.622 + 0.0021$ Year; $F_{1,43} = 10.50$; $r^2 = 0.196$; $p = 0.0023$; Table 1, Fig. 4).

The best model to explain changes in annual abundance of teal in February relative to numbers in December only retained an effect of hunting ($F_{1,46} = 10.55$; $r^2 = 0.19$; $p = 0.0022$; Table 1). The relative abundance of teal in March compared to December was 0.39 (± 0.03, n = 34 years) before the ban on February hunting, and 0.59 (± 0.05, n = 14 years) after hunting ceased in 2002 – an increase of 1.5 times (Fig. 4).

March abundance of teal was correlated with February abundance (within-year correlation: $r^2 = 0.29$, $p = 0.0002$).

Table 1. Summary of the backwards stepwise model selection process for abundance of teal in Camargue in February or in March relative to December numbers of the same winter. For each variable its partial F and p values upon removal are indicated, as well as the order in which each variable was removed from the initial full model (1 = first removed). The variable kept in the final model is indicated in bold. See text for description of the variables.

	Models for February abundance of teal			
Variable	F	p-value	df	Order removed
Year × Hunting	0.0430	0.8369	1	1
Year	0.0122	0.9125	1	2
February abundance year n-1	0.0924	0.7627	1	3
Hunting	**10.5533**	**0.0022**	**1**	**not removed**
	Models for March abundance of teal			
Variable	F	p-value	df	Order removed
Year × Hunting	0.4437	0.5103	1	1
Hunting	0.1942	0.6624	1	2
March abundance year n-1	0.7626	0.3888	1	3
Year	**10.5006**	**0.0023**	**1**	**not removed**

Discussion

The present results show an increase in the use of the Camargue by teal in late winter, with the numbers of individuals present during February compared to the annual December peak numbers being 1.5 times greater over the period 2003–2019 than the period 1964–2001, and a more gradual increase for March data. Interestingly, for February such change occurred in a stepwise manner after hunting was completely banned during that month. As such, this result supports the hypothesis that a cessation of hunting lead to a greater use of the region by waterfowl during that crucial part of the year that is the beginning of spring migration. In March the mean abundance was lower and more variable, and only a gradual increase over the years was recorded.

Indeed, the explanatory power of our final models was low (r^2 values around 0.2), indicating that other factors contribute to drive the abundance of teal in the Camargue during late winter. Although the European population size of teal has clearly increased over the last decades (Wetlands International 2017) this is unlikely to explain the observed pattern, which is an increase in the proportional number of teal in February or March compared to December numbers of the same winter, not straight bird numbers. Climate warming and changes in agricultural practices may have made the Camargue more attractive to waterfowl than it was in the past (Guillemain et al. 2010, 2015), which may have contributed to greater abundance of teal during late winter. Climate warming alone is however unlikely to explain the pattern observed, because it is actually expected to cause earlier spring migration departure and earlier arriving on breeding grounds in birds, as documented by Lehikoinen and Sparks (2010) for birds in Europe and similarly for green-winged teal *Anas carolinensis* in North America (Schummer et al. 2017), while the opposite was recorded here.

As explained in the methods, the aerial surveys covered all areas where teal could be present during the day in the Camargue delta, so the observed results are not a mere local redistribution from alternative local habitats. That the best model for teal abundance in February only retained an effect of hunting ban provides support for that the change in legislation was followed by greater local abundance. Currently,

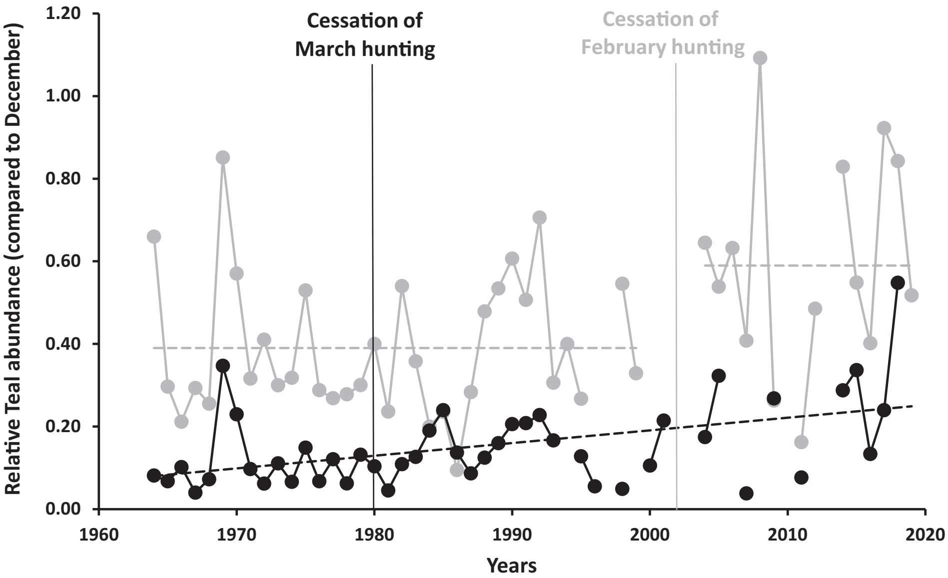

Figure 4. Changes in the relative abundance of teal in Camargue during March (black dots and lines) and during February (grey) compared to previous December numbers. The dotted lines show the best fitting models: a gradual increase over years for March data, a step increase after hunting got banned for February data (proportions are presented here to ease reading, but analyses were performed on logit-transformed data, see text).

we cannot assess which teal are increasingly using the Camargue during late winter; these could be the local wintering teal lengthening their stay, or birds coming north from the south-west (e.g. in Spain) increasingly using the area as a migration stopover. Both of these non-mutually exclusive hypotheses would be made possible by the safer current conditions allowing an efficient use of the existing local food resources, now that there is no hunting during these months. However, teal have been ringed in large numbers in the area since the 1950s and continue to be so. A companion study will compare monthly turnover rates during February and March over the years (see the existing turnover rate and stopover duration estimates in teal from ringing data in Pradel et al. 1997, Choquet et al. 2013), and assess whether the observed pattern results from an extended stay of the wintering birds, or an increase in the late winter stopovers. The positive correlation between March and February abundances recorded here may support that there is an extended stay of the ducks during late winter, although the modest r^2 value indicates there are other factors at play. In parallel, the analysis of the ringing data may allow for testing of an alternative hypothesis that the increased numbers of birds in February simply result from late winter birds no longer being harvested and being taken out from the population. Accordingly, the hypothesis would predict that an increase in teal survival rates should be observed over the last 70 years.

The current results are in line with the conclusions of the IPBES that human harvest and its associated consequences (management of hunting habitat, disturbance, etc.) are still currently a major driver of wildlife abundance and distribution, despite other large-scale environmental changes (IPBES 2019). The results for March are less conclusive, because hunting ban was not retained in the best model. However, during that month too a greater abundance is currently recorded compared to what it was in the past, and the cessation of March hunting may have contributed to increased teal abundance in March.

The most likely hypothesis to explain the current patterns in numbers is therefore that the cessation of hunting has allowed a greater use of local habitats by teal, especially in February, permitting birds to access the food resources that were available in the Camargue but hardly accessible when disturbance was too high (Tamisier and Dehorter 1999, Brochet et al. 2009).

The disturbance effect of hunting on waterbird habitat use has long been demonstrated: the creation of new hunting reserves usually leads to increases in local waterfowl numbers (Bellrose 1954, Madsen and Fox 1995, Madsen 1998, Guillemain et al. 2002, Tamisier et al. 2003, Fox and Madsen 2017; in Camargue: Mathevet and Tamisier 2002), although this may be restricted to the protected areas themselves (Väänänen 2001, Brochet et al. 2009). Intermittent hunting periods have also been shown to translate into successive phases of concentration of birds into reserves versus hunted areas locally (Cox and Afton 1997). The shortening of the hunting season in France over the last 65 years constitutes a unique natural experiment on the consequences of hunting for habitat use by spring migrating ducks. The present results also support the hypothesis of Tamisier and Dehorter (1999) that the number of birds in the Camargue is limited by local hunting pressure, at least for these months of the winter. That such an increase is particularly evident for February can be explained by the flux of individuals over the Camargue likely being large during February, which corresponds to the beginning of spring migration (Guillemain et al. 2006), while the passage of teal has already largely faded during March in southern France.

The present results have obvious consequences in supporting current European policy of banning hunting at the onset of spring migration. Indeed, this allows a greater use of the habitats by migratory individuals at the beginning of the migration episode (a 50% increase). The current results also have habitat management implications: the Camargue now has a growing responsibility towards birds during late winter, as it hosts increasing numbers of individuals when they prepare for migration and the coming breeding season. Earlier studies suggested a positive link between the body condition of teal during late winter and their subsequent breeding success (Tamisier and Dehorter 1999, Guillemain et al. 2008, see also the effect of spring hunting on goose body condition in Mainguy et al. 2002). The safer prolonged access to the Camargue during late winter may translate into a more efficient use of existing feeding grounds and food stocks, hence have positive impacts onto population dynamics (Madsen and Fox 1997). It is therefore the responsibility of the local land managers to provide adequate foraging conditions to teal during February and March. It is a common practice that Camargue hunting grounds are drained after the end of the season, either for agricultural purposes (e.g. ricefields, Niang et al. 2016) or to dry natural marshes in order to prevent colonisation by exotic weeds and/or promote mineralisation of the sediment (Vallecillo et al. 2019). The current results however suggest that some wetlands should also continue to be managed in a suitable way that follows the natural rainfall regime, allowing parts of these areas to remain flooded for one to two months after the closure of the hunting season and providing a mosaic of habitats to suit the various water needs of wildlife during late winter, including species whose hunting is no longer practiced during such periods.

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Data availability statement

Data can be requested through Jocelyn Champagnon at Tour du Valat (champagnon@tourduvalat.org).

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Appendix 1. Completion of the aerial waterfowl surveys. Surveys were done monthly from September to March, 1964–2019; a cross in the cell indicates a missing count.

Season	SEP	OCT	NOV	DEC	JAN	FEB	MAR
1964–1965							
1965–1966							
1966–1967							
1967–1968	x						
1968–1969							
1969–1970							
1970–1971							
1971–1972							
1972–1973							
1973–1974							
1974–1975							
1975–1976							
1976–1977							
1977–1978							
1978–1979							
1979–1980							
1980–1981							
1981–1982							
1982–1983							
1983–1984							
1984–1985							
1985–1986							
1986–1987							
1987–1988							
1988–1989							
1989–1990							
1990–1991							
1991–1992							
1992–1993							
1993–1994							
1994–1995							x
1995–1996	x						
1996–1997	x	x				x	
1997–1998				x			
1998–1999							
1999–1900							x
2000–2001						x	
2001–2002						x	
2002–2003	x	x	x	x	x	x	x
2003–2004	x	x	x	x			
2004–2005			x				
2005–2006		x					
2006–2007							x
2007–2008							
2008–2009							x
2009–2010							
2010–2011		x	x	x			x
2011–2012	x				x		
2012–2013	x	x					x
2013–2014		x	x	x			x
2014–2015							
2015–2016							
2016–2017							
2017–2018	x	x	x				
2018–2019							
2019–2020							x